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GENETICS

# of PITCH PINE

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Research Paper
WO-27

U.S. Department of Agriculture
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GENETICS OF PITCH PINE

APR 11 2014

Reference Abstract

Ledig, F. Thomas, and John H. Fryer.

1974. Genetics of pitch pine. USDA For. Serv. Res. Pap. WO-27, 14 p.

Although the relative importance of genetic and environmental effects has scarcely been tested, pitch pine, *Pinus rigida* Mill., appears to be an extremely variable species. In colonial times, intensive utilization may have resulted in dysgenic selection. Natural hybrids with pond, loblolly, and shortleaf pines are suspected, and controlled crosses have been successful with these and several other species. The major role of pitch pine in tree improvement has been as a source of cold resistance in crosses with less hardy pines.
OXFORD: 174.7: *Pinus rigida:* 165.3, 165.5, 165.6, 165.72
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Research Summary
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Pitch pine, *Pinus rigida* Mill., is complex in its taxonomy. It is closely related to pond pine and to several other species with which it hybridizes naturally or can be crossed by the breeder. As a result of its extensive natural range, many disjunct stands, the diversity of its sites, and its recent evolutionary history, there is considerable variation, revealed both in native stands and in uniform-garden plantings. Most notable is the occurrence of a dwarf form in the New Jersey Pine Plains.

Pitch pine is sexually precocious and moderately prolific, with rapid and good germination being typical. Severe inbreeding depression results from selfing. There is variation in several reproductive features such as the age at which cones are borne and the frequency of serotinous-coned trees.

It can reproduce by sprouts, an adaptation to fire. Rooting of cuttings is feasible, particularly with scions from young trees or with the sprouts that appear after fire or logging. Graft incompability may be less of a problem than with many other conifers, and grafting can be done with ease.

Pitch pine will probably not be a major pulp or timber species, but it is a potential contributor of genes for cold hardiness and site tolerance to such species as loblolly pine. It has direct value in conservation and amenity plantings. Historically, pitch pine has been one of the most exploited of American forest trees. Perhaps the highest present priority should be the study and preservation of its diverse natural populations before they are irrevocably lost.

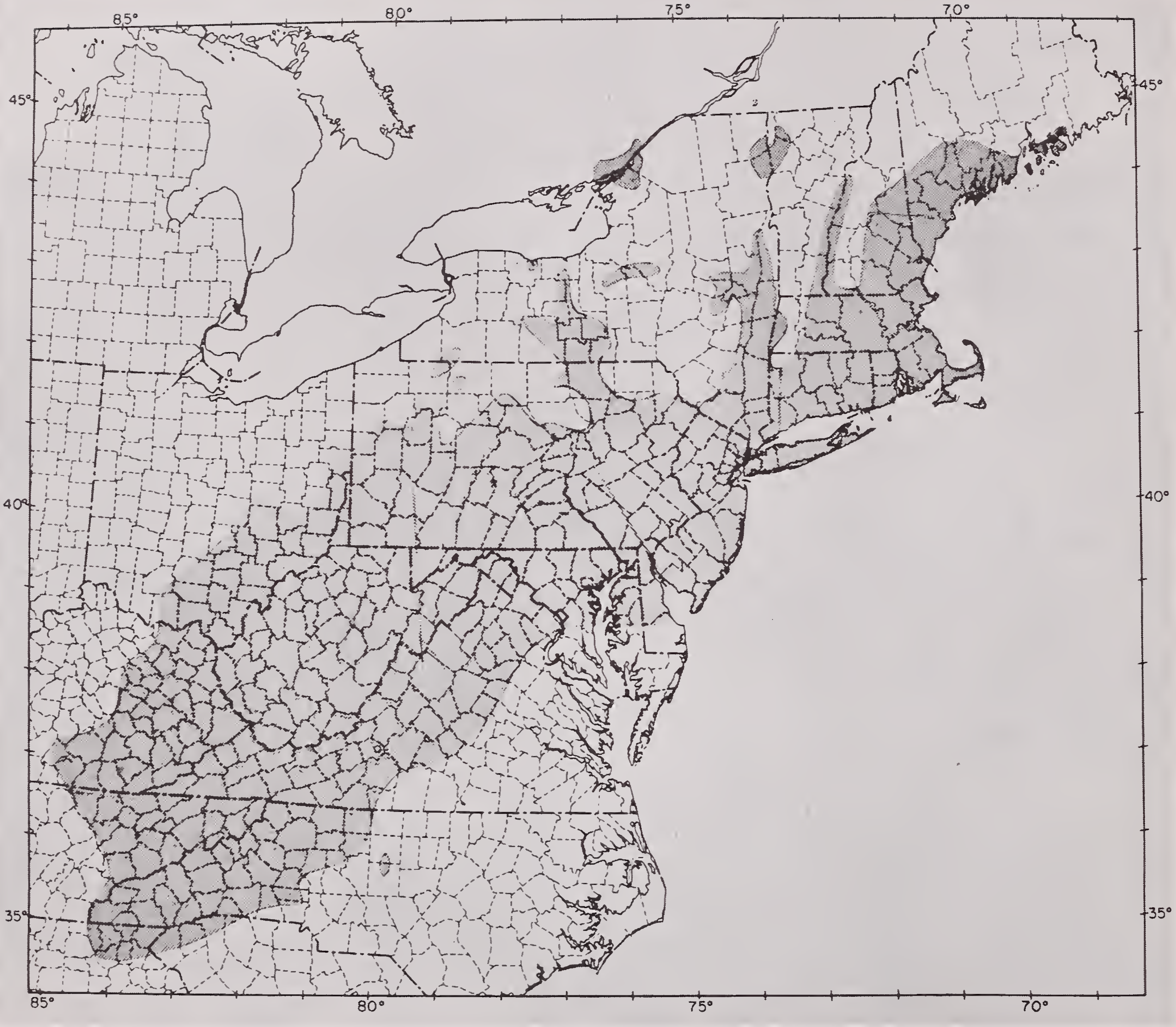

Figure 1.—Range of pitch pine, exclusive of pond pine (modified from Critchfield and Little 1966).

GENETICS OF PITCH PINE[1]

F. Thomas Ledig and John H. Fryer[2]

INTRODUCTION

Pitch pine, *Pinus rigida* Mill., is the only member of the southern yellow pines (subsection *Australes* Loud.) that is native in most of the northeastern United States. It is cold-hardy, remarkably resistant to drought and fire, and tolerant of salt spray. While it is attacked by several insects, it is not overly susceptible to these pests. It is well adapted to the infertile soils on many pine sites in the Northeast, and has been tested and recommended for planting on other adverse sites (both droughty or poorly drained), such as those found on strip mine spoils, on coastal sand dunes, and in the Tennessee Copper Basin where sulfur dioxide is an injurious agent (Allen 1950; Fernald 1945; Committee on Site Classification, Northeastern Forest Soils Conference 1961). In many situations it has survived well and grown at an acceptable rate but has developed branchy, crooked stems (e. g., McQuilkin and McNamara 1967).

Poor form is, indeed, a characteristic of pitch pine over most of its range. The species is also prone to epicormic branching, and its growth rate declines at an early age. The extent to which these traits are heritable is still uncertain. It seems likely, however, that pitch pine will be valuable in tree improvement as a source of genetic variation utilizable in hybridization programs with pines of better form.

Pitch pine has been perhaps the most over-exploited species of all North American trees. In addition to being cut for piling, construction lumber, and flooring, it was the first American pine to be felled or tapped for naval stores. Early tapping (by the destructive method of "boxing") was so intensive that laws were passed as early as 1709 to reduce pressure on the pineries.

Immense numbers of the trees were also cut for domestic and industrial fuel, for the high extractive content causes the wood to burn bright and hot. By 1812 pitch pine was eliminated from Nantucket Island, primarily because of fuelwood consumption, and was then reintroduced in plantations (Yates 1960). On other offshore islands it became and has remained extinct (e. g., Lewis 1924).

Pitch pine is of importance as a store of genetic variability that can readily be transferred to other southern pines through hybridization. Yet, after 300 years of short-rotation exploitation, it is not unlikely that present stands are a result of severe dysgenic selection. There is a real possibility that populations with perhaps unique and valuable gene complements will soon join the already extinct, offshore island populations and that this store of variability will be lost. The 1,800 square miles (4,660 square *km*) of pitch pine in the Pine Barrens of New Jersey are threatened by urban developments of various sorts. As an aid to conserving some of the world's forest tree gene resources, provenances representing the entire range will be preserved for a few additional decades in field tests initiated by one of us (F. T. L.) and sponsored by the American Philosophical Society.

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[1] A revision and updating of Fryer and Ledig (1971). Preparation of this paper was financed by Grant No. 30 of the Michaux Fund of the American Philosophical Society. We gratefully acknowledge the advice and counsel of S. Little, Principal Silviculturist, USDA Forst Service, Pennington, N. J.

[2] Respectively: Associate Professor of Forest Genetics and graduate student, Yale University, School of Forestry and Environmental Studies, New Haven, Conn.

TAXONOMY

Pinus rigida Mill. was first described in 1768. It has been known under the synonyms *P. frazeri* Loddiges, *P. loddigesii* Loudon, *P. canadensis trifolia* Du Hamel, *P. serotina* Long, *P. taeda* var. *rigida* Aiton, and probably many others (Dallimore and Jackson 1948; Gordon and Glendinning 1858).

In Shaw's (1914) classification, *P. rigida* was placed in the subgenus *Diploxylon*, subsection *Pinaster,* group *Insignes,* the closed-cone pines. When Duffield (1952) reclassified the subgenus on the basis of crossability patterns and similarities in oleoresins, he included *P. rigida* in his group XI, along with slash and Caribbean pines (at that time both *P. caribaea,* now *P. elliottii* var. *elliottii* and *P. caribaea),* longleaf pine *(P. palustris* Mill.), shortleaf pine *(P. echinata* Mill.), loblolly pine (*P. taeda* L.), spruce pine (*P. glabra* Walt.), West Indian pine *(P. occidentalis* Sw.), and pond pine *(P. serotina* Michx.) A recent classification by Critchfield and Little (1966) retains essentially the same grouping under the subsection *Australes* Loud. but includes Table-Mountain pine *(P. pungens* Lamb.) and Cuban pine *(P. cubensis* Griseb.) in addition to the species of Duffield's group XI.

At various times, pond pine was considered a variety of pitch pine and until recently was included in standard texts as *P. rigida* var. *serotina* (Michx.) Loud. (Harlow and Harrar 1950). Clausen (1939) identified pond pine as a subspecies, *P. rigida* ssp. *serotina* (Michx.), and Smouse (1971) concurs.

Though pitch pine exhibits diverse forms and grows over a wide range of adverse sites, it has only one named variety. *P. rigida* var. *lutea,* distinguished by its reddish-yellow, thin bark and deep yellow heartwood, grows mixed with typical pitch pine in Fairfield County, Ohio (Kellerman 1892). On the basis of an individual tree, a globose pitch pine was named *P. rigida* forma *globosa* (Allard 1940).

RANGE AND HABITAT

The natural range is depicted in figure 1. South of Maryland occurrence is restricted to the mountains and the western edge of the Piedmont, but distribution tends to be very patchy or discontinuous. Extensive stands are found only in the northeastern portion of the range on the Coastal Plain or on glacial outwash plains. Previously published range maps have indicated outliers in western Kentucky and central Georgia, but native pitch pine probably does not occur in these areas. In addition, it has been rumored to occur along the coast as far as southern New Brunswick (Morton and Lewis 1917) although repeated inquiries have failed to verify that it now grows in coastal Canada.

Pitch pine tolerates a wide variety of climates but appears to prefer high humidity and well-distributed rainfall. It is commonly restricted to the less fertile sites, particularly sandy or gravelly soils, shallow soils, and rocky outcrops. In Maryland, Delaware, New Jersey, New England, and eastern New York, it is found in greatest abundance on glacial outwash plains and coastal sands. West of this area it is most common on the shallow soils of ridges and on dry southern exposures. While it endures a wide variety of soil moisture conditions, and grows in or adjacent to swamps containing such mesic species as Atlantic white-cedar, *Chamaecyparis thyoides* (L.) B.S.P., it is generally considered a xeric species.

Its virtual absence from good sites is explained not by any lack of ability to grow there, but rather by its strong intolerance of hardwood competition and possibly by a requirement for fire for regeneration. In all mature stands that we have observed, pitch pine is rapidly replaced by hardwoods when fire has been excluded.

Biogeography

Distribution and evolution of pitch pine, as of other northeastern species, was profoundly influenced by the Wisconsin and earlier glaciations. Fossil and pollen deposits indicate that pines are probably now as far north as they have ever been in their history (Mirov 1967). The adaptation of pitch pine to Coastal Plain soils, and its tolerance of fire, enabled it to migrate north on the sterile outwash plains left by retreating glaciers.

Refuges for pitch pine are uncertain. The continental shelf off the southern Atlantic coast, exposed by a drop in the ocean level, may have served as a source of pitch pine for post-glacial migration northward. Migration occurred along the Coastal Plain and up the river bottoms of New England, particularly through the Hudson, Connecticut, and Merrimac River Valleys. Another refuge was the foothills south of the Appalachians. Migration northward was predominantly along the ridges through Pennsylvania and western New York. Speculation upon variation due to the original source of migration and subsequent evolution is largely fruitless in the absence of adequate fossil records and experimental evidence.

SEXUAL REPRODUCTION

Reproductive Development

Pitch pine is monoecious. Sexual maturity is attained early. Two-year-old seedlings have produced male strobili as well as female strobili that developed into cones yielding viable seed (Andresen 1957). In an extreme case, female strobili have developed on 12-month-old (Namkoong 1960) and 9-month-old potted seedlings (unpublished observations). Vigorous stump sprouts may bear cones in 4 years, but quantity production usually does not occur until 8 to 12 years of age (Little 1965b). There is a great deal of variation in cone production over the range of pitch pine. On Cape Cod, Mass., it is common to observe seedlings under 6 feet tall carrying over 50 cones, whereas heavy cone crops are rare for most trees in Georgia. Cones tend to be persistent, remaining attached to the branch for many years. Coning has an irregular periodicity, but there is probably a good crop every 3 years on the average (Little 1965b).

As in other pines, primordia are initiated the year preceding emergence of the cone (Hong and Lee 1970; Hong et al. 1971). Development is of the classic pine type. In fact, details of reproductive development in *Pinus* were worked out in pitch pine and described in the pioneer work of Ferguson (1904). In an attempt to induce male sterility in order to facilitate mass hybridization, Hong (1963) tested the effect of many growth regulators on development of the male gametophyte, but none was successful. Hong (1967) also studied amino acid composition of fresh and germinating pollen. Phenylalanine, not detectable in mature pollen, appeared in extracts of germinating pollen. Other amino acids increased in quantity during germination. Loblolly and pitch pine differed in that each had one unique amino acid (unidentified).

Ovulate cones occur in one, and less commonly, in two clusters on a shoot. In the latter case, the cone is said to occupy a "lateral" as well as the "terminal" position common in pines (Shaw 1907). The cones are borne on successive cycles of growth (sometimes miscalled internodes) arising from the polycyclic winter bud (Tepper 1963). Two clusters of cones are most common on the Coastal Plain but occur throughout the range. There is evidence that cones in the two whorls do not reach maximum receptivity at exactly the same time.

Pollen is shed and females are receptive for a period of 1 to 2 weeks. Dates are around April 29 to May 11 in the mountains of North Carolina (Dorman and Barber 1956), between May 3 and May 20 in the Coastal Plain of New Jersey (Little 1941), and in late May to June in east-central Pennsylvania (Schaeffer 1949). When grown in New Jersey, grafted clones from the northern limit of the species' range are receptive earlier than local trees (S. Little, USDA Forest Service, personal communication, 1971).

Pollen is distributed by wind, and outcrossing is the rule. Unlike red pine, *P. resinosa* Ait., the only other hard pine with which it is associated in the Northeast, pitch pine suffers severe inbreeding depression. Progeny produced by selfing are decidedly inferior to those from wind-pollination (Wright 1962). Inbreeding also reduces seed yield (Critchfield 1963). However, a certain amount of natural selfing probably occurs, as suggested by a small proportion of aberrant phenotypes in the progeny of open-pollinated trees.

Cone and Seed Production

Cones mature in the fall of the second year after pollination. Seedfall generally begins in early November and is 90 percent complete within 2 months (Little 1965b), although there is much local variation. Perry (1922) reported that in Pennsylvania little seed was shed until January. If cones are collected in early or mid-October, germination will generally be high. Cones collected September 9 at an elevation of 1,400 feet (427 meters) in southern Pennsylvania were very green (specific gravity greater than 1.0), but they nevertheless opened normally and the extracted seed germinated as rapidly and as completely as that from mature, dry cones collected more than a month later.

While most cones open readily on the tree or can be opened after collection by drying at 30°C, some trees bear serotinous cones that do not release seed until subjected to high temperatures or years of weathering. Such cones can be opened by quickly dipping them in boiling water to melt the resin that bonds the scales together. Serotinous cones appear to be an adaptation to fire, ensuring seed shed at the most opportune time for regeneration in terms of site availability. Serotiny in pines is probably controlled by a single pair of major genes (Sittman and Tyson 1971). In pitch pine, serotiny is largely restricted to the Coastal Plain and decreases in all directions from the New Jersey Pine Plains (Ledig and Fryer 1972). The Pine Plains themselves are areas of dwarf forest predominantly 1 to 2 m in height, largely of coppice origin, subjected to frequent and extreme fires, and occupying about 15,000 acres (6,000 ha) within the Pine Barrens (McCormick and Buell 1968). Cone serotiny approaches 100 percent. Andresen (1963) termed the Pine Plains population a pyrotype or pyric ecotype.

Data on seed yields and seed weights were collected in 1969 and 1970 as part of the American Philosophical Society's range-wide study of pitch pine. These are presented, along with values from the *Woody Plant Seed Manual* (USDA Forest Service 1948), in table 1. More localized collections by Toumey and Stevens (1928) and Andresen (1963) fell within the ranges indicated in table 1. The overall mean values are 74 seeds per cone of which 73 percent are filled—a sound-seed yield of 54 per cone. Yield is lower in cones from the upper third of the crown than from the lower two-thirds. Within the cone, most sound seed is found within the middle third (McIntyre 1932).

Among stands, there is a threefold variation in mean sound-seed weight, and among trees the range is more than sevenfold. Definite geographic trends occur. Northern stands have many light seeds per cone. There is a decrease in number and concomitant increase in mean seed weight toward the South and West, but total weight of sound seed per cone remains nearly constant.

Most lots germinate very rapidly, and stratification appears unnecessary (Heit 1961 and personal observations). Although Barton (1930) reported that stratification speeded germination, only one lot benefited from stratification in the New York State seed testing laboratories (Heit and Eliason 1940). Most seed begins germination in 7 days. Cold storage for several years does not decrease rate or total germination when moisture content is maintained at 4 to 5 percent (personal observation). Seed stored open has retained high germinability for 3 years (Toumey and Stevens 1928). Germinability from serotinous cones declines somewhat with age of the cone, at least over the first 4 years after maturity (Andresen 1963).

Germination is good at temperatures from 15° to 30°C, being most rapid at 25°–30°C.

TABLE 1.—*Seed yields for pitch pine*

Source of information	Seed weight per 100 kg cones	Seeds per kg[1]	Total Seeds per cone	Sound Seed
	Kg	*M seeds*	*No.*	*Percent*
American Philosophical Society Rangewide Collection				
Range among stand means	—	66.4–200.8	28–117	32-95
Range among tree means	—	40.0–294.1	3–151	6–99
Mean	—	117.6	74	73
Woody Plant Seed Manual				
Range	—	79.4–184.0	—	—
Mean	2.0–3.0	136.7	—	84

[1] For the American Philosophical Society data, figures refer to sound seeds only.

Lower or higher temperatures are inhibitory. Provenances apparently do not differ in their temperature requirements (Fryer and Ledig, unpublished data).

Effect of Ionizing Radiation

In a series of publications, Mergen and coworkers have reported the effects of ionizing radiation on reproductive potential of stands, germination of seed, cytology and growth of seedlings, and effect of seed handling on the results of irradiation treatment in pitch pine (Mergen and Stairs 1962, 1963a, b; Mergen and Johansen 1964; Mergen and Cummings 1965; Mergen and Thielges 1966). These reports have demonstrated a retardation in reproductive phenology, increase in chromosome aberrations, decrease in pollen germination, depression in seed germination and reduction in hypocotyl length, high mortality of vegetative primordia and initial increase in sprouting, and many morphological abnormalities attributable to the lethal effects of irradiation on cells. After 10 years of sublethal exposure to gamma irradiation, seed set dropped from 0.76 per cone scale to 0.08 (Sparrow et al. 1965).

Controlled Pollination

Techniques for controlled pollination are the same as those employed for other southern pines (Wakeley and Campbell 1954). Female strobili are isolated in viscose sausage casing bags supported with silicon-aluminum rods and pollen is introduced by hypodermic syringe. In Korea, higher seed yields were obtained with both polyethylene and paper bags than with sausage casing (Hyun 1970b). Adding boric acid to the pollen, or spraying solutions of indoleacetic acid on the receptive strobili did not improve seed set (Hyun 1970b). Pollen will retain high viability if stored deep-frozen (Duffield and Callaham 1959). In mass-pollination trials, loblolly pine pollen was applied to pitch pine strobili with an insecticide duster; the yield was 2.5 hybrid seeds per cone (6.2 percent of the total seed) as compared to 13 hybrids per cone from controlled pollination of isolated females (Hyun 1970b). Squirrels destroy some cones, but enclosing second-season cones in a cloth bag seems to discourage predation.

ASEXUAL REPRODUCTION

Sprouting

Pitch pine has a remarkable ability to sprout from dormant buds after fire and logging (figs. 2, 3). Stumps of 20- to 30-year-old trees may produce the greatest number of sprouts (Fairbrothers and Andresen 1957). Seedling sprouts eventually outgrow those from older trees, and the slowest growing are those from very old stools, such as in the Pine Plains (Little 1965b). Sprouting may be the most important factor in the fire resistance of pitch pine (Little and Somes 1956). The Pine Plains is largely a forest coppiced by fire. Early in its ontogeny, the seedling develops a basal crook that eventually results in two reciprocal bends at nearly right angles to the stem axis (Little and Mergen 1966). Growth in diameter presses the underside of the trunk into the forest floor, where it becomes buried. Dormant buds on the underside of this bend are insulated even from hot fires.

Rooting

Pitch pine can be rooted with difficulty. Of cuttings from succulent stump sprouts of a 30-year-old tree, 66 percent rooted (after treatment with Hormodin No. 3,[3] but no rooting occurred if the sprouts had hardened off (Santamour 1965). In a study by Hyun and Hong (1968) rooting ability declined with age of the ortet, and cuttings from the lower third of the crown rooted better than those from the upper crown. These authors also found that cuttings collected early in the growing season (March and April for greenhouse stock) were far superior to those collected later. When cuttings are from very young seedlings (10 days old), roots arise from the pericycle in the manner of normal branch roots rather than from callus (Hong and Hyun 1970).

Pitch pines vary in ability to yield rooted cuttings at a given age, and physiological and biochemical differences have been demonstrated between easy- and difficult-to-root genotypes. A low nitrogen level was associated with trees producing easy-to-root cuttings. (Yim 1962; Hyun 1967; Hyun and Hong 1968). Difficult-

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[3] Mention of trade names is for information only and does not imply endorsement by the U. S. Department of Agriculture.

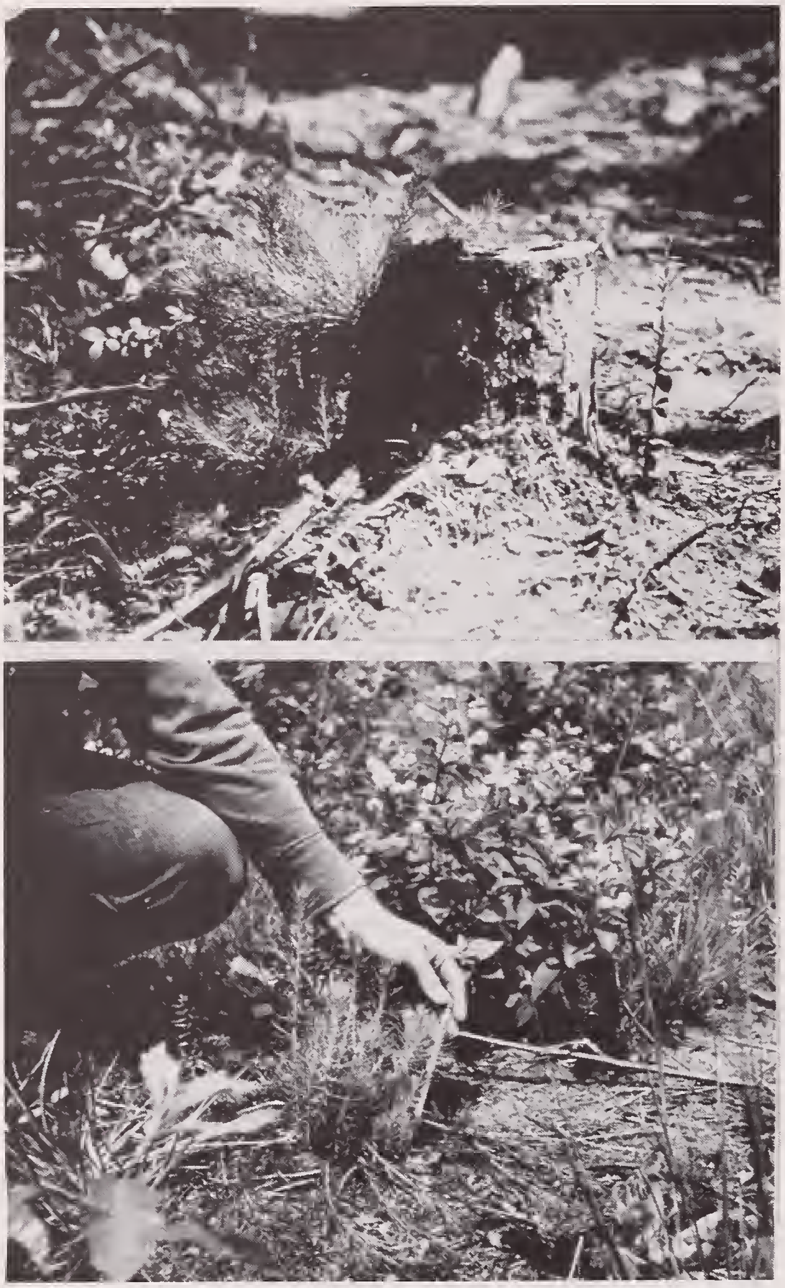

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Figure 2.—Sprouting in pitch pine. *Above:* *stump* sprouts. *Below:* sprouts from root crown after above-ground portions were consumed by fire.

to-root trees had higher concentrations of alanine, leucine, phenylalanine, threonine, valine, and γ-aminobutyric acids; these amino acids proved inhibitory to root initiation in mung bean. Two growth promoters and two growth inhibitors were extracted from pitch pine, and their relative amounts in cuttings and the balance and interaction between them were considered by Hyun and Hong (1968) to cause differences in rootability among trees. Later, Hong (1969) found that both promoters and inhibitors aided root formation in bioassays with mung beans and pine hypocotyls. Brachyblasts induced by decapitation of the terminal had higher levels of the promoters than normal shoots and rooted more easily.

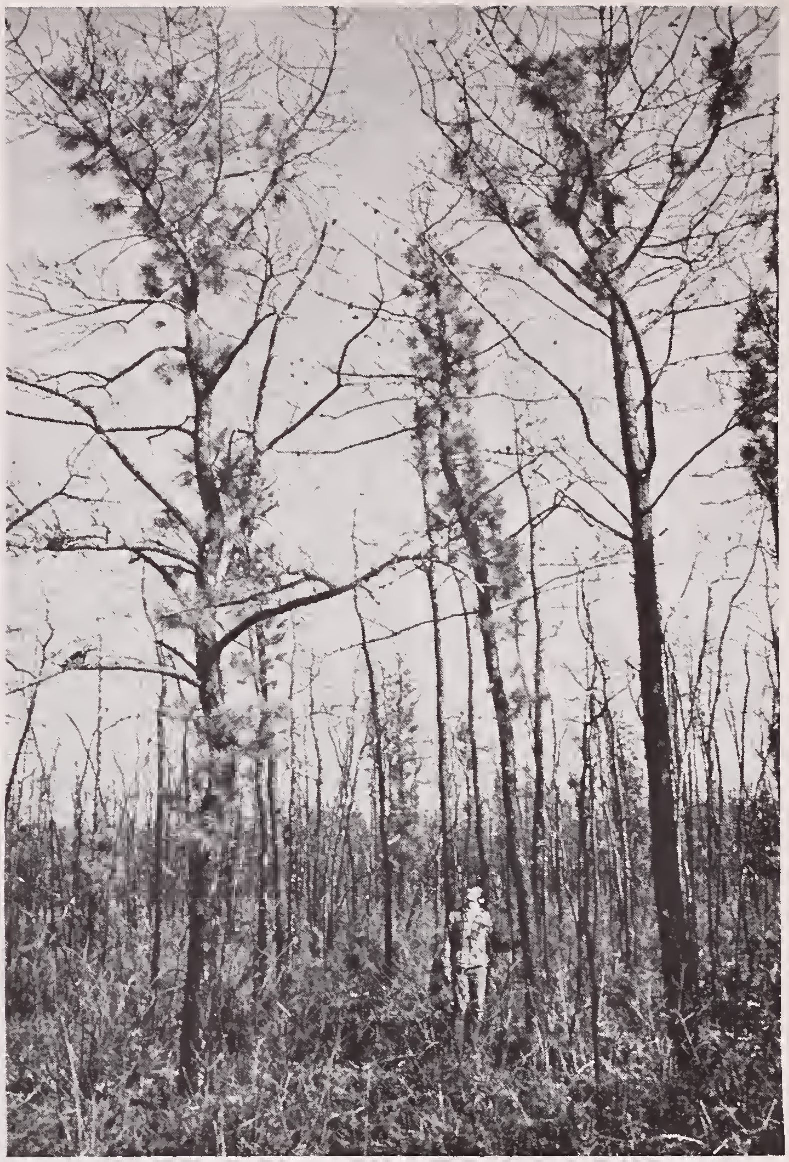

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Figure 3.—Epicormic branching in pitch pine after a fire that destroyed the foliage.

Grafting

Grafting is easy, and side or cleft grafts may be made in the field. The scion should be protected with polyethylene bags and kraft covers. Little[4] has noted much less incompatibility and overgrowth in grafted pitch pine than in loblolly pine in the same orchard. Scion material stores well at 0 to 5°C for up to 2 months, and preliminary investigations have indicated that success in grafting is associated with a high C/N ratio in the scion material (Choi 1967). Heteroplastic grafting of pitch pine was carried out with loblolly, Japanese red *(P. densiflora* Sieb & Zucc.), Japanese black *(P. thunbergiana* Franco), and Korean *(P. koraiensis* Sieb. & Zucc.) pines as stock, and pitch pine has served as a rootstock for the latter three plus slash pine (Mergen 1954; Choi 1967; Kim 1969; Little[4]).

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[4] Little, S. 1969. Progress report on breeding work with pitch and loblolly pines at New Lisbon, N.J. Unpublished report on file by USDA Forest Service, Northeastern Forest Experiment Station, Upper Darby, Pa. 16 p.

GENETICS

Phenotypic Variation

As a result of either phenotypic plasticity, genetic variation, or both, pitch pine is an extremely variable species. It grows as a prostrate shrub behind the dunes on Fire Island, N.Y., and on the New Jersey Pine Plains it is a dwarf 20 inches to 13 feet (0.5 to 4 m) tall. Less than 22 miles (35 km) from the Pine Plains it approaches 100 feet (30 m) in height. Andresen (1959) suggested that the dwarf form is merely a result of environmental modification, a pseudo-nanism. Because trees in the Pine Plains are pollinated by surrounding stands of larger trees, Little and Somes (1964) also thought it unlikely that the dwarf characteristic was genetic. However, 7 years after treatment to convert coppice stands in the Pine Plains to natural stands of seedling origin, the pitch pines on the regeneration plots were still dwarf, while white pines interplanted on other plots were growing rapidly.[5] Genetically dwarf shoots are known from somatic mutations induced in pitch pine by chronic gamma irradiation (Sparrow 1966).

At the northern extreme of its range, pitch pine has a maximum height near 33 feet (10 m) and diameter of 12 inches (30 cm), while at the southern extreme it attains heights over 80 feet (25 m) and diameters near 30 inches (75 cm). Though the species is characterized by poor form over most of its range, relatively straight trees are common in northeastern New York and in Ohio and Kentucky. More than 50 years ago Illick (1919) called attention to the fine form of pitch pine native to the Michaux State Forest in Pennsylvania and advised it as a seed source for reforestation, but its genetic superiority remains to be proven.

Cone length and width and seed size are smallest in the Northeast and increase toward the South and West. Tree-to-tree data on cone size and shape were taken by Perry and Coover (1933), who commented on the uniformity within trees of pitch pine as compared to shortleaf. Variation in cone form was known among introductions in Britain (Bean 1909). Cones of coastal populations may be larger than those of either inland or dune formations (Harshberger 1916). Number of sound seeds per cone decreases from northeast to southwest. As has been mentioned, nearly all the trees in the New Jersey Pine Plains have serotinous or closed cones, and the frequency decreases in concentric rings around the Plains (Ledig and Fryer 1972). However, occasional trees with serotinous cones occur throughout much of the range and are locally common, especially in Pennsylvania.

Wood properties show similar clearly defined trends. Mean tracheid length increased from 3.0 mm in Maine to 3.6 mm in Kentucky, and mean extracted specific gravity over the same range increased from 0.42 to 0.53 (Ledig, Zobel, and Matthias, in preparation). A similar trend for specific gravity was found by Saucier and Clark (1970), who sampled the entire commercial range of pitch pine, and by Markwardt and Wilson (1935), who sampled only a few trees in Massachusetts and Tennessee. Although there were correlations with latitude and longitude, Saucier and Clark (1970) interpreted the variation pattern as ecotypic and separated populations occurring on glacial outwash plains in New York and New England from those on Appalachian ridges further south. In contrast, there are no apparent geographic trends in pond pine (Taras and Saucier 1970).

Whether such variation is genetic awaits intensive provenance study. At Yale University, a range-wide collection of pitch pine has been made, totaling 6 parent trees in each of 64 stands extending from Canada to Georgia. A nested sampling scheme has been devised to allow estimation of effects due to differences among regions, among stands within regions, and among open-pollinated progenies within stands. Outplantings are planned in New Jersey, Massachusetts, Connecticut, Nebraska, and Korea, and additional investigations will be carried out in controlled environments.

Genetic Variation

A small provenance experiment was established in 1966 with 1–2 nursery stock at the Harvard Black Rock Forest, Cornwall, N.Y. (Jack Karnig, personal communication), with additional outplantings at Greenbank, N.J., and Petersham, Mass. Four sources, in unreplicated row plots, were included in each planting. The planting at Cornwall was destroyed by deer, but both of the other two tests indicated that two Burlington County, N.J., sources were superior in height growth to sources from Cape Cod and Cornwall. A provenance test in Canada was mentioned by Farrar (1947), though no details were given. In nursery phases of the American Philosophical Society's rangewide test in Connecticut, height was inversely correlated with latitude of origin, and after two winters there was no sign of cold damage to any of the provenances.

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[5] Little, S. 1971. Progress report on converting low sprout stands of pitch pine and scrub oaks to pine seedlings. Unpublished report on file by USDA Forest Service, Northeastern Forest Experiment Station, Upper Darby, Pa. 19 p.

Genetic variation in response to photoperiod was shown for provenances from New York (44°N latitude) and North Carolina (35°N latitude). Response of New York seedlings to artificially prolonged days was greater than that of seedlings from North Carolina, as measured by increased height or dry weight growth (Vaartaja 1959). Under short days, seedlings from New York set bud sooner than seedlings from North Carolina.

In a controlled environment, variation occurs in photosynthetic rate (Ledig, in preparation) and in isozyme composition of leaves and roots (Fryer, in preparation). Northern populations seem to have more forms of various enzymes and more variation among trees than southern populations.

Cytogenetics

The karyotype of pitch pine is similar to that of other pines in its subsection (Kim 1963; Yim 1963). There are 11 pairs of chromosomes with median centromeres and 1 pair, the shortest, with a submedian centromere. Secondary constrictions occur in some pairs, but not consistently (Yim 1963, and personal observation). Saylor and Smith (1966) studied chromosome behavior during meiosis (see below, under Control-Pollinated Hybrids).

Polyploids have been induced in pitch pine by colchicine treatment, and they were as inferior in growth and as aberrant in morphology as polyploids observed in other members of the genus (Kim et al. 1967). However, in a study by Hyun and Kim (1963) some colchicine-induced tetraploids in the *P. rigida* × *(P. rigida* × *P. taeda)* backcross were equal to the diploid in growth rate. Spontaneous polyploids have also arisen in backcross progeny and have been intensively investigated (Hyun, Kim, and Lee 1967). Some were tetraploids, and all showed some deformity of leaf morphology or anatomy. Among hybrid seedlings, spontaneous tetraploids occurred in a frequency of 0.06 percent (Kim and Lee 1968). For both pitch pine and the backcross of the pitch × loblolly hybrid, stomates were larger and fewer in number and tracheids were larger in diameter and length in the tetraploids than in diploids (Hyun and Kim 1963). Tetraploids produced pollen with reduced viability and slower tube growth (Hyun, Kim, and Lee 1967).

Natural Hybrids

Pitch pine is generally acknowledged to form natural hybrids with shortleaf, pond, and loblolly pines, and hybrids with Table-Mountain pine are suspected (P. E. Smouse, personal communication, 1970). The occurrence of hybrids between pitch pine, on the one hand, and pond and loblolly pines, on the other, was described in detail by Little et al. (1967). Pitch pine is sympatric with pond and loblolly pines only in the extreme southeastern portion of its range, but a broad and extensive zone of intergradation seems to occur in eastern Maryland and Delaware. Clausen (1939) reported gradation between pitch and pond pines in New Jersey. It is not certain whether intergradation between pitch and pond pines is the result of recent hybridization or of incomplete speciation. In Smouse's study (1971), pitch and pond pines were scored on a discriminant function and found to intergrade clinally through a transitional population in Cape May County, N.J. and the Delaware-Maryland-Virginia Peninsula. Morphological affinities were computed for each pair of taxa in the pitch, pond, loblolly, and shortleaf complex; pitch and pond pines were much more similar than any other pair. Smouse concluded that pitch and pond pines were more distinct than varieties but were not of specific status. He agreed with Clausen (1939) in denoting the two as subspecies.

Pitch and shortleaf pines occur sympatrically over a large area. Natural hybrids have frequently been inferred (Austin 1929; Illick and Aughanbaugh 1930; Little and Somes 1951). Hybridization with pitch pine is suspected for one seed source of shortleaf pine in the Southwide Pine Seed Source Study (Wells and Wakeley 1970).

Smouse (1971) determined that there was little barrier to artificial crosses or their reciprocals between pitch pine on the one hand and pond, loblolly, and shortleaf pines on the other. Critchfield (1963) also considered this a particularly crossable subgroup of the eastern *Australes*. There appears to be no substantial phenological barrier between pitch pine and any of the other four species with which hybridization is suspected. In their areas of sympatry all have maximum pollen shed and female receptivity in the second and third weeks of May (Little 1965b).

Control-Pollinated Hybrids

The first control-pollinated hybrid of pitch pine, *P. rigida* × *P. taeda*, was made in 1933 at the Institute of Forest Genetics, Placerville, Calif., and was backcrossed to pitch pine in 1942 (Liddicoet and Righter 1960). Additional successful hybrids of pitch pine have been produced at the Institute with pond and shortleaf pine (Critchfield 1963). Needle anatomy of pitch × loblolly hybrids was on the whole intermediate, while pitch × pond hybrids resembled pitch pine rather closely (Keng and Little 1961). However, monoterpene composition of the pitch × pond hybrid is intermediate between that of the parental taxa (Smith 1967). Botanical descriptions of all these controlled pitch pine hybrids have been published (Little and Righter 1965).

When pitch pine was crossed with pollens of loblolly pine sampled from 22 sources throughout the range, no differences in seed set were attributable to pollen source (Hyun and Hong 1969; Hyun 1970a). In a Korean nursery, hybrids grew most rapidly when the pollen parent was from Florida or the Gulf Coast, but the trees suffered winter injury. Hybrids produced by pollen from seven sources of loblolly west of the Mississippi were inferior to other provenances in height growth. As evaluated by height and cold hardiness of the hybrids at 5 years of age, the best pollen sources were northern Mississippi, North Carolina, Virginia, and New Jersey.

The pitch and loblolly pine hybrid has been produced on a mass scale in Korea, where it was given the binomial × *P. rigitaeda* (Hyun and Ahn 1959a). About a dozen years ago, 11,000 to 30,000 pollination bags were being placed annually in 10- to 14-year-old pitch pine plantations. Two to three bags were mounted on each tree, mainly in the upper crown. A mean of 20 sound seeds per cone, representing about 30 percent of the normal yield from open, intraspecific pollination, was obtained in some years (Hyun and Ahn 1959a; Hyun 1962a, b). In other programs, mean yield of sound seeds per cone has run as high as 40 for specific individuals (S. Little, personal communication, 1972).

The Korean hybrids of pitch and loblolly pine were intermediate between their parents in needle characteristics (length, width, fascicle sheath length, and color) and in speed of germination and coldhardiness. In anatomical characteristics they were closer to one or the other parent (Shibata 1968). Cone and seed characteristics resembled those of pitch pine (Hyun and Ahn 1959b), while tracheid length was closer to that of loblolly pine (Koo and Hong 1967). The karyotype of the hybrid was investigated by Kim (1963), but since parental karyotypes were indistinguishable, the hybrid karyotype was not distinct. The backcross of the hybrid with pitch pine or loblolly pine is more fertile than the cross of pitch with loblolly pine. Backcrosses to loblolly pine are distinctly less coldhardy than the F_1 hybrid, though their growth rate is similar to the F_1 (Hyun et al. 1965). Backcrosses to pitch pine are more coldhardy than the F_1, although more slower growing and of poorer form.

A putative hybrid of pitch and Monterey (*P. radiata* D. Don) pines has been produced by the Korean Institute of Forest Genetics at Suwon. When first attempted, the cross was very fertile (Hyun 1956), yielding 30 percent viable seed. In subsequent trials it proved more difficult, giving 3 percent or less of sound seed (Hyun, Koo, Hong, and Lee 1967). Cytological investigation indicated a complete breakdown of nucellar development and pollen tube growth in most cases (Hyun and Yim 1963), with an occasional fertilization followed by difficulties in the zygotic stage (Hyun and Lee 1965). The surviving pitch × Monterey hybrids were intermediate between their parents in cone, seed, and needle characteristics (Hyun, Koo, Hong, and Lee 1967). Though the hybrid was reported to be coldhardy and to have slightly more rapid growth than pitch pine, personal communication with S. K. Hyun indicates that it has little promise. If in fact the putative hybrid is verified, it is of major botanic interest because it forms the only link between subsections *Australes* Loud. and *Oocarpae* Little and Critchfield.

Other apparently successful controlled hybridizations were the cross of pitch pine with Japanese red pine of subsection *Sylvestres* Loud. and with slash pine, belonging to the same subsection as pitch pine (Ahn 1963). Crosses of red × pitch pines and Austrian (*P. nigra* Arnold) × pitch pines were unsuccessful because of the inability of foreign pollen tubes to penetrate the nucellus, an indication of definite incompability (McWilliam 1959). The cross of pitch pine with the knobcone × Monterey hybrid (*P. attenuata* × *radi-*

ata) also failed (Heimburger 1969). Smouse (personal communication, 1970) reports the pitch × Table-Mountain pine cross successful, although more difficult than the crosses with pond, loblolly, or shortleaf pines.

Meiosis in various hybrids, including those with pond, shortleaf, and loblolly pines, and for the double cross of (shortleaf × loblolly) × (pitch × loblolly) was observed by Saylor and Smith (1966). One pitch × pond hybrid showed a high frequency of lagging chromosomes at telophase II. On the average, the hybrids had slightly higher pollen abortion and meiotic irregularity than the parental species, indicating only slight cytological barriers to hybridization.

BREEDING AND TREE IMPROVEMENT

The most phenomenonal use of pitch pine in tree improvement is the mass hybridization with loblolly pine practiced routinely in Korea. Plus trees of pitch pine for both hybridization and mass intraspecific pollination were selected from the numerous plantations of this species in Korea (Choi and Kim 1963). The hybrid has better growth and form than pitch pine, yet retains sufficient cold-hardiness to survive throughout Korea while loblolly pine is restricted to the southern coast. Currently, extensive use is being made of seed produced by wind pollination of the F_1 growing in plantations or in seed orchards where it is interplanted with pitch or loblolly pines. The progeny of the F_1 are nearly as fast-growing and cold-hardy as the F_1 itself (Hyun 1970b). Because inferior F_2 segregates or backcrosses will be eliminated naturally by competition, the final stand will be composed of the most rapidly growing and cold-hardy trees.

The suitability of some of the hybrids for afforestation has been investigated in the United States. The hybrid with pond pine was very similar to pitch pine in form and growth rate, and the shortleaf × pitch hybrid was of poorer form and growth than the shortleaf parent (Little and Righter 1965). When outplanted in Korea and Illinois, the early pitch × loblolly hybrids were superior to pitch pine in growth and form (Hyun 1956; Lorenz and Spaeth 1953). They did not grow as rapidly as loblolly pine, but they survived winters in which loblolly was badly damaged. North of the 39° N latitude in Illinois, the hybrid outgrew both loblolly and pitch pines, and had excellent survival and form, but in one plantation was severely damaged by sapsuckers (Bey and Lorenz 1970).

Pitch × loblolly hybrids planted in Maryland and New Jersey were no better than native pitch pine (Little and Somes 1951), but Little[6] attributed this performance to poor selection of parent trees. In Mississippi, 6-year-old pitch × loblolly hybrids from unknown parental sources grew slowly even by comparison with the pitch pine parent (Schmitt 1968). Performance was also poor for hybrids of pitch pine from New Jersey with pond pine from Florida, and for a double cross of (pitch × loblolly) × (shortleaf × loblolly), in the plantation measured by Schmitt. The pitch × loblolly cross is promising in Canada, although it is hardy only in southern Ontario and cannot tolerate calcareous soils (Holst and Heimburger 1969).

Currently, S. Little, of the Northeastern Forest Experiment Station, and L. F. Trew, of Westvaco, Inc., are engaged in a program of selection and subsequent hybridization in loblolly and pitch pines. A grafted orchard has been established in New Jersey with approximately 30 clones each of phenotypically superior loblolly pine from Delaware and Maryland and pitch pine from Virginia northward (Little 1965a). The orchard was designed to facilitate controlled hybridization and not for the natural exchange of pollen between the two species. Some initial pollinations were made in 1968 and outplanting trials have begun. The objective is "to produce a source of high-quality, locally adapted pines for most sections of the Northeast" through hybridization or selection within species.

Georgia Kraft Company and Union Camp Corporation are also testing the loblolly × pitch hybrid for its ability to grow on shallow soils and in areas of environmental extremes (North Carolina State University Cooperative Tree Improvement and Hardwood Research Programs 1972). In Wisconsin, pitch pine is being hybridized with sand and spruce pines to provide combinations for poor sites (Lester 1970.)

Twenty-one pitch pines had been selected for the North Carolina seed orchard program by

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[6] Little, S. 1964. Master plan for breeding and testing pitch-loblolly pine hybrids, selected loblolly pine, and selected pitch pines. Unpublished report on file at the USDA Forest Service, Northeastern Forest Experiment Station, Upper Darby, Pa. 26 p.

1971 (North Carolina State University Cooperative Tree Improvement and Hardwood Research Programs 1971), and the State Forest Service had completed a grafted orchard with 13 ramets each of 16 clones of pitch pine at Crossnore (Clark 1970). Pennsylvania also has a grafted orchard of select trees (Winieski 1965). Region 7 of the National Forests has included pitch pine in its improvement program (Hunt 1965).

In tree improvement, stem and crown characteristics should be of primary importance in selection of pitch pine plus-trees. Pitch pine frequently has a sinuous or crooked stem combined with heavy and steeply angled branches, and produces abundant epicormic sprouts when grown at wide spacings. These characteristics are major reasons for its underutilization. The chief importance of pitch pine in tree improvement will probably be either as a source of genetic variation utilizable in hybridization programs with pines of better form, or as a species for adverse sites. There will be ample variation upon which to base a tree improvement program if a significant sample of the present populations can be preserved.

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Ledig, F. Thomas, and John H. Fryer.
1974. Genetics of pitch pine. USDA For. Serv. Res. Pap. WO-27, 14. p.

Although the relative importance of genetic and environmental effects has scarcely been tested, pitch pine, *Pinus rigida* Mill., appears to be an extremely variable species. In colonial times, intensive utilization may have resulted in dysgenic selection. Natural hybrids with pond, loblolly, and shortleaf pines are suspected, and controlled crosses have been successful with these and several other species. The major role of pitch pine in tree improvement has been as a source of cold resistance in crosses with less hardy pines.

OXFORD: 174.7: *Pinus rigida*: 165.3, 165.5, 165.6, 165.72
KEYWORDS: *Pinus rigida*, pitch pine, genetics, tree improvement, geographic variation, racial variation, hybridization

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